The Effect of Wave Impact on Some Aspects of the Biology of Sea Mussels

BY

J. R. E. HARGER

Department of Biological Sciences, University of California at Santa Barbara [1]

(9 Text figures; 15 Tables)

INTRODUCTION

The absence of a simple wave impact measuring device has hampered the efforts of ecologists in comparing conditions among different intertidal habitats for some time. Moore (1935) has made use of the percentage of the year's winds blowing into the angular aperture of a locality; Southward (1958) used the occurrence of waves washing over the breakwater at Plymouth, coupled with known wind records, to generate a wave index; Ballantine (1961) has outlined a biologically defined exposure scale for the comparative description of rocky shores; and finally Eifion Jones & Dometropoulos (1965) have used an apparatus consisting of a drogue attached to a spring dynamometer to record drag produced by passing waves.

(I) MEASUREMENT of WAVE IMPACT

In investigating the effects of wave action on the biology of two species of mussels (*Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837) on the coast of Southern California, I made use of a device for measuring wave impact. This consisted of a smooth 6 inch long nail, a spring steel "c" clip, and a metal plate of 1/16 inch gauge steel. A $\frac{1}{4}$ inch diameter hole was drilled in the center of the plate which was then passed up the nail shaft until it rested against the head. A "c" clip was then threaded up the shaft of the nail to the bottom of the plate so preventing the plate, when released, from falling down the nail (Figure 1). The nail was then fixed into an "intertidal" rock or pier piling so that the head, and metal plate supported by the "c"clip, projected into the prevailing wave motion. Wave action, during one tidal period, then forced the metal plate and "c" clip down the shaft of the nail. The distance through which the plate is moved depends on 3 factors: size of the plate, frictional resistance afforded by the "c" clip, and strength and frequency of wave impact.

The first 2 factors can be controlled; all that is necessary is to insure that such a combination of plate size and clip strength is used, at a particular geographic location, that the plate will not be forced completely down the nail during one tidal period. The force exerted by heavy storms can be estimated with this device, simply by making the plate very small.

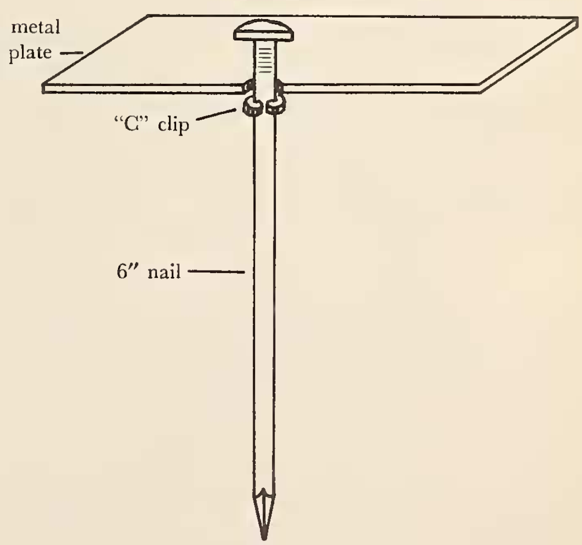

Figure 1

Wave impact measuring device

[1] Present address: Department of Zoology, University of British Columbia, Vancouver 8, British Columbia.

The force of wave impact for one (or more) tidal cycles is calculated in the following manner:

a = area of the plate in cm^2

f = force required to overcome the friction of the "c" clip, measured by pulling it down the nail with a spring balance (in kg)

d = distance the plate is moved (in cm)

Wave force = $(f/a)d$. kg-cm/cm^2

If the wave force is to be compared at several locations, nails must be set out at each place within the same tidal period. (I found that an individual "c" clip could be used only 2 or 3 times and that the nail shafts must be kept free of burrs and nicks.) Table 1 lists values obtained for wave impact, over three 24-hour periods, from 5 locations.

These areas are all situated within a few miles of the City of Santa Barbara, on the coast of Southern California (Figure 2). Stearns Wharf is located at the entrance

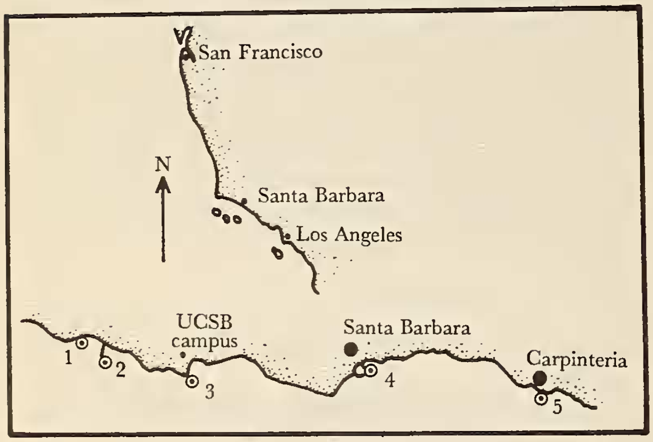

Figure 2

Location map showing Santa Barbara and study areas
1. Ellwood Rocks 2. Ellwood Pier 3. Goleta Point
4. Stearns Wharf 5. Carpinteria

of the Santa Barbara harbor and is quite sheltered. Ellwood Pier (property of Signal Oil and Gas Co.) is a large pier, almost ½ mile in length, situated some 14 miles west of Santa Barbara, on open sandy shore. The steel pilings of this pier extend from the intertidal surf zone out to a depth of about 40 feet. These pilings support large intertidal clumps of mussels which are comprised of both *Mytilus californianus* and *M. edulis*. Ellwood Rocks are part of the shore line immediately adjacent to Ellwood Pier, and Goleta Point is an outcropping of rock just below the campus of the University of California at Santa Barbara (10 miles west of the City of Santa Barbara). These points were chosen for easy access and because a series of exposures ranging from sheltered (Stearns Wharf) to exposed (Goleta Point) were obtained.

During the recording period, winds were light (5 - 8 knots on-shore) but a heavy swell was running producing breakers between 4 and 5 feet in height on the local sand beaches. From Table 1, it appears that the force of wave impact suffered by Ellwood shore is 4 - 5 times that incurred by the outer end of the adjacent Ellwood Pier. Within the pier itself, a particular sheltered position (intake pipe) received less than ½ as much force as nearby open pilings and Goleta Point experienced some 13 to 18 times more wave impact than the Ellwood shore.

The recorders at Ellwood Shore were driven into the front face of a 3 foot high hemispherical boulder (8 feet in diameter) which projects from the relatively gently sloping lower mid-littoral (the recorders in all locations were placed in the lower mid-littoral). The recording site at Goleta Point was a 5 foot high vertical rock face situated in the lower mid-littoral region. This rock face is so placed that a swell hitting it at half tide may throw spray to a height of 12 to 15 feet.

These measurements indicate that the impact force experienced by any group of organisms on an exposed shore line depends on the strength of the waves, on the aspect of the rock face to which they are attached, and on whether there is a beach, or other rocks, to seaward which can absorb some of the force before the waves reach the organisms. There is a large difference between the exposure value obtained from Stearns Wharf (sheltered) and that from Ellwood Shore (exposed) (see Table 1). However, on the open shore, rocks in different positions (Ellwood Rocks and Goleta Point), are exposed to wave impact forces which differ from each other by as much as the difference between the sheltered harbor (Stearns Wharf) and the stretch of exposed coast (Ellwood Rocks) impact values. Taking into account the difference between the front (seaward) and rear (landward) faces of intertidal rocks, it is clear that the intensity of wave impact on an exposed intertidal shore must vary greatly. Wharf pilings projecting from natural intertidal regions suffer more from wave impact than deep water pilings. This difference between deep and shallow water pilings has also been reported by Bascom (1964). On pilings, in general, wave impact is greatest at the mid-tidal level and less at higher and lower levels.

A method similar to that reported here of recording the pressure exerted by waves against structures was used by Thomas Stevenson in 1842. Bascom (*op. cit.*) reports

Table 1

Mean wave impact values obtained on three days from four different sites

(The unit of measurement is kg-cm/cm²)

Place	12 Dec. 1966 Mean Wave Impact Values	12 Dec. 1966 Sample Size	13 Dec. 1966 Mean Wave Impact Values	13 Dec. 1966 Sample Size	15 Dec. 1966 Mean Wave Impact Values	15 Dec. 1966 Sample Size
Stearns Wharf, Santa Barbara Harbor	0.012	3	0.014	3	0.022	3
Ellwood Pier (Intake Pipe)	0.048	4	0.055	1	0.060	1
Ellwood Pier (Outer Pilings)	0.105	2	0.152	5	0.199	4
Goleta Point	$<$3.769	6	9.160	3	9.187	3
Ellwood Rocks	0.495	5	0.590	5	0.766	6

that the instrument used "... consisted of a plate six inches in diameter facing into the waves, mounted on a stiff horizontal spring. Behind the spring was a rod held by a friction grip in such a fashion that it would move as the plate moved but remain at the maximum distance which the plate pushed it. As each increasingly large wave impacted against the plate, the rod would be pushed to a new position. The distance moved times the spring constant gave the maximum wave (single) force exerted on the plate ..." The modern "professional" pressure gauge which is now used by engineers to measure the force exerted by waves on pilings, piers and shoreline structures is described by Bascom (*op. cit.*) as "consisting of a stack of thin plates of tourmaline crystal set in a strong metal case. When subject to pressure, this gage produces a small charge of electricity which can be amplified ..." In the same book, data which indicate that there is a substantial increase in the force exerted on a piling as waves change from swell into breakers and then foam-lines are presented. Bascom also comments that "measurement of wave forces on pilings is complicated by the continual reversal of direction of the water as the crest moves in one direction and the trough moves in the other. ..."

Table 2

Comparison of growth increment data: *Mytilus californianus* and *Mytilus edulis* from exposed and sheltered cages set at the mid-tide level on the outer end of Ellwood Pier. The mussels used in the experiment were all originally between 3 and 4 cm long. Growth period was from December 1966 to March 1967

All measurements are in centimeters

Note: one asterisk (*) indicates significance at the 5% level, two asterisks (**) significance at the 1% level and three asterisks (***) significance at the 0.1% level. Abbreviations of statistical terms are those used by J. C. R. Li (1964).

Group	Mean	Standard Deviation	Sample Size	F 3,155
1. *Mytilus edulis* from plastic cage	0.94	0.57	33	45.01***
2. *Mytilus edulis* from wire cage	0.34	0.27	44	
3. *Mytilus californianus* from plastic cage	1.53	0.72	42	
4. *Mytilus californianus* from wire cage	1.44	0.56	40	

Individual D. F. Tests	F 1,155
1.2/3.4	108.56***
3/4	0.55N.S.
1/2	25.92***

The advantages of the wave impact measuring device described in this paper lie chiefly in its simplicity and low cost. By using several instruments at several locations an ecologist can get a quick (although perhaps somewhat rough) estimate of the wave impact force acting on different parts of the intertidal region.

(II) EFFECTS OF WAVE IMPACT ON THE BIOLOGY OF *Mytilus edulis* AND *Mytilus californianus*

(A) Growth

The effect of wave impact was investigated by placing equal numbers of each species of mussel (individuals 3 - 4 cm in length) in open mesh wire cages (exposed treatment) and in cages of partly occluded sheet plastic (protected treatment) and recording subsequent growth. The first type of cage was constructed from ½ inch mesh (1.27 cm) galvanized hardware cloth and was cylindrical in shape (diameter 7 inches {17.78 cm}) with a height of 8.5 inches (21.5 cm). The various components (wire sections, etc) used in construction were laced together with braided nylon cord and the entire structure then coated with epoxy resin. This treatment served to give rigidity to the nylon binding and at the same time to cut down any leaching of zinc ions which might affect the enclosed mussels. The second cage was made of plastic kitchen colanders (10 inches {25.4 cm}) in diameter placed face to face and lashed together at the edges (the maximum diameter of the holes in a colander was ¼ inch {0.963 cm}).

The cages were suspended at the mid-tide level on the extreme outer edge of Ellwood Pier. After 4 months (December, 1966 to March, 1967), the growth increment

Table 3

Comparison of growth increment data:
Submerged *Mytilus edulis* from a plastic cage, a wire cage and a naturally occurring clump of mussels growing on an electrode cable

Original shell length has been used as the independent variable and growth increment as the dependent variable. All measurements were made in centimeters.

Group	Sample Size	Regression Equation	Slopes F 2,96	Adjusted Means at X=6.708	F 2,96
1. Mussels from clump on cable	27	Y=0.005+0.15X	3.04N.S.	1.011	1.96N.S.
2. Mussels from wire cage	33	Y=0.045+0.17X		1.153	
3. Mussels from plastic cage	42	Y=0.491+0.08X		1.046	

Table 4

Comparison of growth increment data:
Submerged *Mytilus californianus* from a plastic cage, a wire cage and from a naturally occurring clump of mussels growing on an electrode cable

Original shell length has been used as the independent variable and growth increment as the dependent variable. All measurements were made in centimeters.

Group	Size Sample	Regression Equation	Slopes F 2,76	Adjusted Means at X=6.261	F 2,76
1. Mussels from clump on cable	11	Y=0.74+0.023X	0.37N.S.	0.879	1.08N.S.
2. Mussels from wire cage	28	Y=0.64+0.072X		1.092	
3. Mussels from plastic cage	43	Y=0.52+0.089X		1.072	

for each mussel was recorded. It was found that the *Mytilus californianus* populations grew much faster than those of *M. edulis* (Table 2). There was no significant difference in the growth rate of *M. californianus* from the different cages, but *M. edulis* from the wire cages grew $\frac{1}{3}$ the amount shown by the animals in the plastic colander. This difference was attributed to the effect of wave impact which presumably acted more severely on the mussels in the wire cage (the openings in the wire mesh account for approximately 92% of the cage surface) whereas the walls of the colanders, because they were constructed of sheet plastic containing relatively small holes (the holes account for approximately 15% of the cage surface) would diminish the impact of breaking waves. The fact that no significant difference in growth can be detected between *M. californianus* from the sheltered and the open cages would seem to indicate that this species is not sensitive to the exposure differences between the two cages. A further test was conducted at the same time to determine the effect these two cages might have on the growth of both species of mussels when placed below low water where the effects of wave impact are absent. An additional comparison was made in this case between the two treatments using caged mussels and mussels growing naturally within submerged clumps attached to insulated cables suspended from the pier. Growth for each species was not detectably different for any of these treatments (Tables 3, 4), which indicates that caging itself does not hinder growth under these conditions.

(B) Size

Figure 3 illustrates the relationship between the maximum size of *Mytilus edulis* occurring naturally at several localities and the corresponding wave impact values. It can be seen that small mussels are associated with high, and large mussels with low values. This relationship is consistent with what one might predict from knowledge of the force required to remove different sized individuals of *M. edulis* from a rock surface. This force was recorded by fastening either a battery clip to, or looping a piece of cord around a mussel and then hooking a spring scale through the clip or a loop on the cord and noting the force required to dislodge the mussel as the scales were pulled firmly away from the rock. Analysis reveals (Figure 4, Table 5) that the force necessary to tear loose the two species of mussels was significantly different, with *M. californianus* requiring more force when similar sized mussels are compared. Data relating to a third species of mussel, *Septifer bifurcatus* (Conrad, 1837) are also included with the analysis given in Table 5 and illustrated in Figure 4. These mussels occur intertidally on the Santa Barbara coast but are physically quite small – the maximum length attained being about 3.5 - 4.5 cm long. The

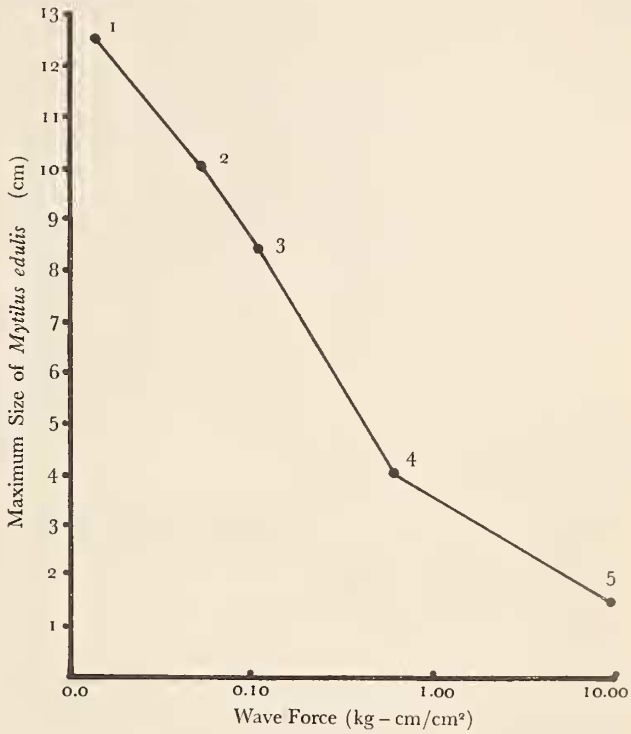

Figure 3

Relationship between wave impact values and the maximum size of *Mytilus edulis* occurring at the measurement sites
1. Stearns Wharf 2. water intake pipe at Ellwood Pier 3. outer end of Ellwood Pier 4. Ellwood Shore 5. Goleta Point

force required to remove an individual from a rock face is greater than that required to remove a similarly sized *M. californianus* individual. (Populations of *Septifer* are found intertidally only in exposed conditions.)

The relationship indicated for *Mytilus californianus* (Figure 4) is strictly linear, even for the largest mussel tested (10 cm long), but the curve obtained for *M. edulis* flattens out once a length of 4 - 5 cm is reached, so that the force required to remove a 10 cm individual is the same as that required to remove a 5 cm mussel. The larger mussels used to provide points on this curve all came from various positions on Ellwood Pier, some from pilings and some from large subtidal mussel clumps which had formed on zinc electrode cables hung from the pier. Since these cables do not touch the bottom, starfish are unable to find and attack the mussel clumps, so, in

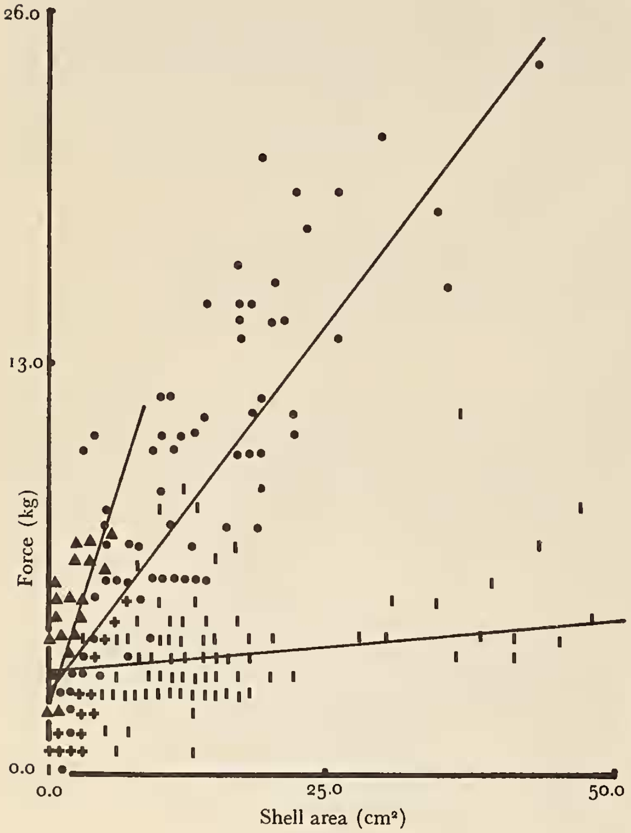

Figure 4

The force to remove mussels from the open shore plotted against a correlate of shell area (length × breadth).
[Shell measurements in centimeters]
Septifer bifurcatus represented by solid triangles, *Mytilus californianus* by solid circles and *Mytilus edulis* by dashes. Crosses indicate values for both *M. californianus* and *M. edulis*. Regression lines are fitted by least squares (see Table 5)

the absence of predation these mussels may reach an extremely large size in the relatively quiet water (*M. californianus* up to 30 cm and *M. edulis* up to 15 cm long). Only mussels unencumbered by the byssal threads of others were used in the tests; even so, it might be argued that since the large mussels came from a completely different environment from that of the shore mussels then the relationship in Figure 6 is not representative of a shore population and that it is therefore invalid to draw inferences from it reflecting the disposition of such populations. It was however impossible to find large individuals of *M. edulis* on the shore, therefore, sub-tidal specimens were used. In an attempt to counteract the above objection a laboratory test was performed, the results of which are presented in Table 6 and Figure 5. Individuals of both species were placed for 3 weeks on the bottom of tanks containing running sea water. The force required to remove them at the end of this time was then recorded. The relationship is essentially the same as that obtained by using the naturally set animals, however, since these mussels established fewer byssal threads the dislodging force was generally lower.

Since small *Mytilus edulis* survive wave impact with apparent success, a comparison of the two species involving animals of up to 4 cm in length was also made. The results show clearly that even at this size *M. californianus* holds on more strongly than does *M. edulis* (Table 7).

From these results one might predict that only small individuals of *Mytilus edulis* could survive in "exposed" situations and that conversely large specimens (5 cm and over) would be likely to occur in sheltered places such as harbors, etc. This is borne out by observations along the coast of Southern California. *Mytilus californianus* on the other hand is able to attach itself such that a relatively constant force (in proportion to its shell area)

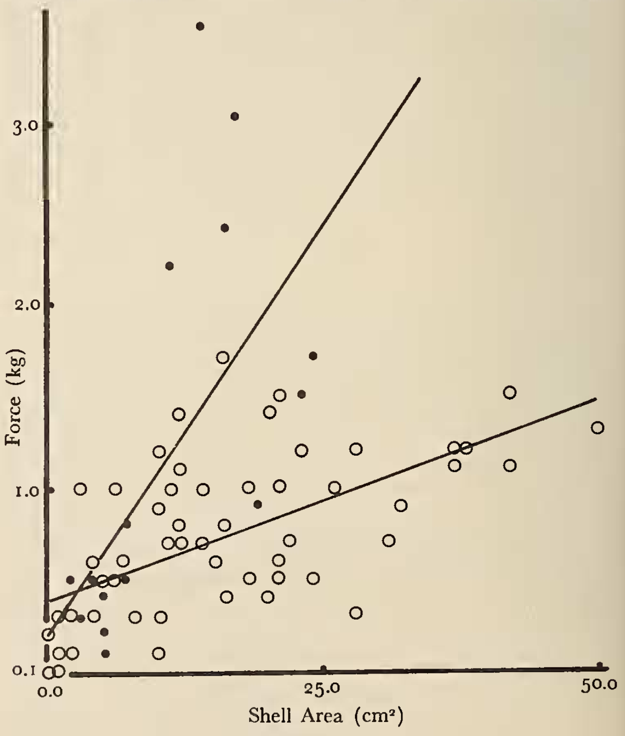

Figure 5

Force to remove mussels from laboratory tanks (constructed from resined fibre glass) plotted against a shell area correlate (length × breadth). ● – *Mytilus californianus;* O – *M. edulis.*
Shell measurements in centimeters

Table 5

Comparison of the force required to remove different sized, naturally set, individuals of *Mytilus californianus*, *Septifer bifurcatus* and *Mytilus edulis*

A measurement correlated with shell area (length × breadth) has been used as the independent variable and force required to remove mussels (measured in kilograms) the dependent variable.

The breadth measurement was made across the broadest part of the shell valves (from the dorsal to the ventral edges): length was measured as the maximum distance between the anterior and posterior edges of the valves, *i. e.*, from hinge(umbo) to siphon regions. All measurements were recorded in centimeters.

Group	Sample Size	Regression Equation	Slopes F 2,262	Adjusted Means at X = 6.261	F 2,262
1. *Septifer bifurcatus*	32	Y = 1.71 + 1.14X	134.28***	14.513	138.01***
2. *Mytilus californianus*	111	Y = 2.14 + 0.58X		8.768	
3. *Mytilus edulis*	125	Y = 3.00 + 0.10X		4.171	

Individual D. F. Test on B	F 1,262
1/2	2.50N.S.
2/3	262.46***
Individual D. F. Tests on Adjusted Means	
1/2	4.03*
2/3	267.95***

Table 6

Comparisons between the forces required to remove different sized individuals of *Mytilus edulis* and *Mytilus californianus* after both species were allowed to attach to the inside of laboratory tanks

A correlate of shell area (length × breadth) has been used as the independent variable and force required to remove the mussels (measured in kilograms) as the dependent variable. Length measurements made on the mussels were in centimeters.

Group	Sample Size	Regression Equation	Slopes F 1,75	Adjusted Means at X = 14.725	F 1,75
1. *Mytilus edulis*	63	Y = 0.40 + 0.024X	14.12***	0.760	32.08***
2. *Mytilus californianus*	16	Y = 0.20 + 0.090X		1.529	

Table 7

Comparisons between the forces required to remove individuals of *Mytilus edulis* and *Mytilus californianus* from the open shore when both are less than 3.27 cm in length

A correlate of shell area (length × breadth) has been used as the independent variable and force required to remove the mussels (measured in kilograms) the dependent variable. Length measurements made on the mussels were in centimeters.

Group	Sample Size	Regression Equation	Slopes F 1,58	Adjusted Means at X = 2.989	F 1,58
1. *Mytilus edulis*	20	Y = 0.26 + 0.604X	3.75N.S.	2.064	7.50**
2. *Mytilus californianus*	42	Y = 0.28 + 1.183X		3.253	

is necessary to detach it, consequently all sizes (at least those up to 10 cm long and probably longer) are able to withstand wave impact equally well and thus no size limitation seems to be imposed on this species by wave action.

(C) Body Weight

Body weight is a further characteristic of mussels which varies with the force of wave impact. This was demonstrated by collecting a group of mussels from each area in which wave impact data were recorded. After recording individual dry body weights, an adjusted (for shell length) mean dry body weight for each group was determined. Figure 6 shows that the body weight of *Mytilus edulis* varies inversely with the amount of wave impact to which it is exposed.

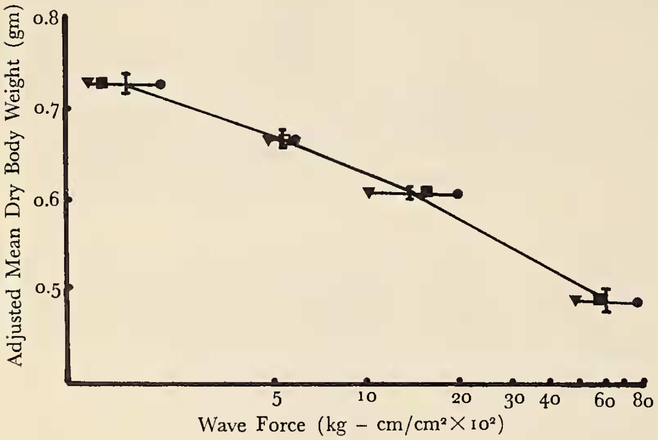

Figure 6

Plot of the square root of dry body weight of *Mytilus edulis* (adjusted to a shell length of 4.037 cm) against wave force values. The latter values were obtained from four geographical positions (Positions 1 to 4 in Figure 3). Values obtained on three different days (▼, ■, ●) are plotted for each position. The bar representing variation of body weight is proportional to twice the standard error of the mean on each side

It was not possible to obtain such a precise relationship for *Mytilus californianus* – it seems that in spite of the amount of wave impact experienced, this species maintains a relatively constant body weight. This is not to say that the body weight of *M. californianus* from different areas is constant, because this is not so. A large amount of variation exists here and the closest thing to a general statement which can be made with regard to this (based on numerous separate samplings from a number of areas) is that the body weight of *M. californianus* from an exposed area (Ellwood Shores) is likely to be less than that from a relatively sheltered area (Ellwood Pier pilings) (Table 8), but this is not always the case.

(D) Production of Check Rings

Both species develop "check rings" the number of which is directly related to the length of the shell. This may be a structural modification conferring additional strength to the shells. In *Mytilus californianus* these rings are numerous and prominent throughout the length of the shell, and give it an appearance much like finely corrugated iron. The shells of *M. edulis* on the other hand, usually have few rings and appear quite smooth in comparison to those of *M. californianus*. For *M. californianus* the number of check-rings per unit length of shell varies

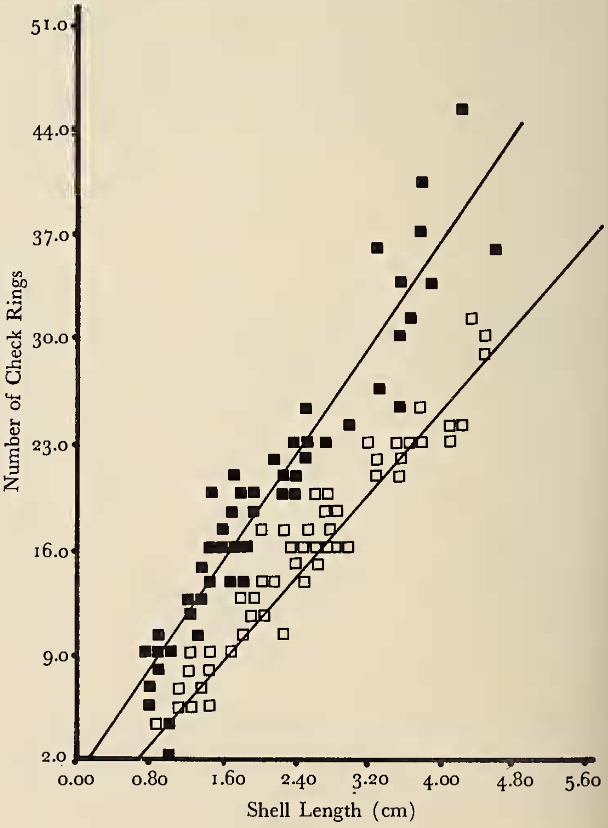

Figure 7

Plot of the number of check rings against shell length for *Mytilus californianus* taken from a clump of mussels at Carpinteria reef. Solid squares represent mussels from the inside of the clump and hollow squares, mussels from outside the clump. Regression lines are fitted by least squares (see Table 9)

Table 8

Comparison of dry body weight data:
Mytilus californianus from two "exposed" positions, Ellwood Shore and Carpinteria Reef and from two "sheltered" positions, Stearns Wharf and Ellwood Pier

The independent variable is shell length (measured in centimeters) and the dependent variable is body weight (in grams). All body weight measurements have been transformed by taking the square root of the variable.

Group	Sample Size	Regression Equation	Slopes F 3,220	Adjusted Means at X = 5.485	F 3,220
1. Ellwood Shore	67	Y = -0.17 + 0.179X	6.34*	0.816	40.75***
2. Carpinteria Reef	74	Y = -0.27 + 0.233X		1.008	
3. Ellwood Pier	57	Y = -0.21 + 0.238X		1.097	
4. Stearns Wharf	30	Y = -0.26 + 0.226X		0.979	

	Individual D. F. Test on B	F 1,220
1.2/3.4		6.37*
	Individual D. F. Tests on Adjusted Means	
1.2/3.4		51.94***

Table 9

Check ring comparison:

Mytilus californianus from inside and outside a clump at Carpinteria Reef

The independent variable is shell length (centimeters) and the dependent variable is the number of check rings.

Group	Sample Size	Regression Equation	Slopes F 1,120	Adjusted Means at X = 3.00	F 1,120
1. Outside	64	Y = -2.05 + 7.05X	22.24***	19.087	290.79***
2. Inside	60	Y = 0.87 + 9.00X		27.884	

Table 10

Comparison of the growth increase shown by two groups of mussels growing inside a plastic colander placed below low water at Ellwood Pier

Members of the first group were originally growing inside a clump of mussels at Carpinteria Reef, those of the second group were outside the same clump. The recorded independent variable was growth increment (in centimeters).

Group	Mean	Standard Deviation	Sample Size	F 1,80
1. Mussels from inside clump	0.59	0.33	38	0.05N.S.
2. Mussels from outside clump	0.57	0.29	44	

with geographical location and even from different situations within a clump of mussels. It seemed that this variation in check-ring frequency was in some way related to the degree of disturbance, harassment or interference that a particular animal had experienced during its growth period.

The first step in testing this hypothesis was to obtain mussels from inside and outside a clump from a moderately exposed shore at Carpinteria Reef (a large flat out-cropping of rock 10 miles east of Santa Barbara). The analysis in Table 9 and Figure 7 shows that mussels on the inside of this clump had more rings per unit length than those on the outside. Mussels from the two samples were then placed in separate plastic colanders which were then lashed together face to face with a plastic divider separating the two resulting compartments. This container was then suspended 3 feet below extreme low water at Ellwood Pier.

After 4 months growth in this sheltered situation the two groups were again examined. The analyses given in Tables 10, 11, and 12 show that:

a) Growth rates of the two groups did not differ from each other.

b) An apparent "basal" frequency of check ring formation was established (i. e., rings within new growth) which was the same for both groups (but differed from the previous frequency established at Carpinteria Reef).

c) This new frequency of ring formation (sheltered position) was much lower than that of either of the original groups (exposed position).

A further experiment at Ellwood Pier designed to compare check ring frequency throughout the intertidal range was established by shaving down a series of large mussel clumps growing on the pier pilings until a single layer of mussels remained attached to each piling. This layer extended from the top to the bottom of the removed clumps (approximately 6 feet or 1.9 m). The mussels comprising this layer were then allowed to grow for 5 months (February to July, 1966). A comparison was then made between the frequency of rings laid down by the mussels when they were confined to the insides of these clumps (before I had removed the outer mussels) and those laid down after they had been exposed. Results indicate that, during the period of exposure, rings developed at a lower frequency per unit length than previously. Mussels higher up the pilings showed higher frequencies than those lower down (both before and after being exposed) (Tables 13, 14, 15). Since mussels from the highest intertidal positions have the lowest growth rates (HARGER, 1967) it seems reasonable to assume that they are developing in positions in which "disturbance" factors (exposure, solar radiation, etc) act with greater intensity and frequency than they would on subtidal

Table 11

Check ring comparison between two groups of mussels growing inside a plastic colander placed below low water at Ellwood Pier

Members of the first group were originally growing on the outside of a clump of mussels at Carpinteria Reef, while those of the second group were inside that same clump. The independent variable is growth increment (in centimeters) and the dependent variable is number of check rings within the new growth.

Group	N	Regression Equation	Slopes $F_{1,78}$	Adjusted Means at X=0.50	$F_{1,78}$
1. Mussels from outside clump	44	Y=1.72+3.53X	0.86N.S.	3.485	3.63N.S.
2. Mussels from inside clump	38	Y=1.26+3.92X		3.222	

Table 12

Comparison of the frequency of check rings laid down by *Mytilus californianus* when growing outside a clump of mussels at Carpinteria Reef with that frequency shown by the same mussels growing within a colander suspended below low water at Ellwood Pier

The independent variable is shell length of the first group and length of new growth for the second (in centimeters). The dependent variable is number of check rings.

Group	Sample Size	Regression Equation	Slopes t $B_1=B_2$
1 Mussels outside clump Carpinteria	64	Y=-2.050+7.047X	2.395***
2. Mussels growing in colander at Ellwood Pier	44	Y= 1.172+3.528X	

Table 13

Comparison of the frequency of check rings laid down by *Mytilus californianus* when growing inside clumps at Ellwood Pier with that frequency shown by the same mussels growing freely on the outside of those clumps

The independent variable is shell length for the first group and length of new growth for the second group (in centimeters). The dependent variable is number of check rings.

Group	N	Regression Equation	Slopes F 1,476	Adjusted Means at X = 2.972	F 1,476
1. Original growth within clumps	240	Y = 8.61 + 4.65X	14.09***	21.97	205.73***
2. Final "free" growth outside clumps	240	Y = 1.75 + 3.02X		10.42	

Table 14

Comparison of the frequency of check rings laid down by *Mytilus californianus* when growing inside mussel clumps high up in the intertidal zone: (Top of mussel clumps at Ellwood Pier, two samples), with that frequency shown by mussels growing low in the intertidal (Inside bottom of mussel clumps at Ellwood Pier, three samples) The independent variable is shell length and the dependent variable is the number of check rings.

Group	N	Regression Equation	Slopes F 4,230	Adjusted Means at X = 4.505	F 4,230
1. Top Pile 27	53	Y = 3.2 + 6.7X	12.50***	33.468	13.82***
2. Top Pile 26	51	Y = 1.5 + 6.8X		32.217	
3. Bottom Pile 27	42	Y = 9.8 + 3.9X		27.452	
4. Bottom Pile 26	62	Y = 7.9 + 4.7X		28.960	
5. Bottom Pile 31	32	Y = 11.2 + 3.6X		27.393	

	Individual D. F. Test on B	F 1,230
1.2./3.4.5		45.99***
	Individual D. F. Tests on Adjusted Means	
1.2./3.4.5		50.55***

mussels. Further to this, a positive correlation may be said to exist between high check ring frequencies and the action of any factor tending to disturb and inhibit growth, i. e., such as found in mussels growing on exposed shores, high up in the intertidal, or in the center of clumps. Mussels in such situations show much higher check ring frequencies than those taken from quiet areas (Ellwood Pier), low positions within the intertidal or on the outside of mussel clumps.

It would seem that 3 separate factors are involved in the formation of check rings on *Mytilus californianus*:

1. There is some inherent ring-laying pattern which operates even in extreme shelter.

2. A mussel growing freely on the outside of a clump may increase its frequency of ring formation in response to periodic disturbances such as heavy waves, unduly low tides, hot weather, etc.

3. Perhaps a mussel confined within a clump, and therefore growing extremely slowly (Harger, 1967), may occasionally experience "favorable" periods in which it is able to grow a little. Such a period might be established by movement of the mussel clump by wave action, so allowing a particular mussel within the clump to be relieved of pressure imposed on it by its neighbors for a short time. Subsequent growth would then give rise to an interval between rings. In this case the rings themselves

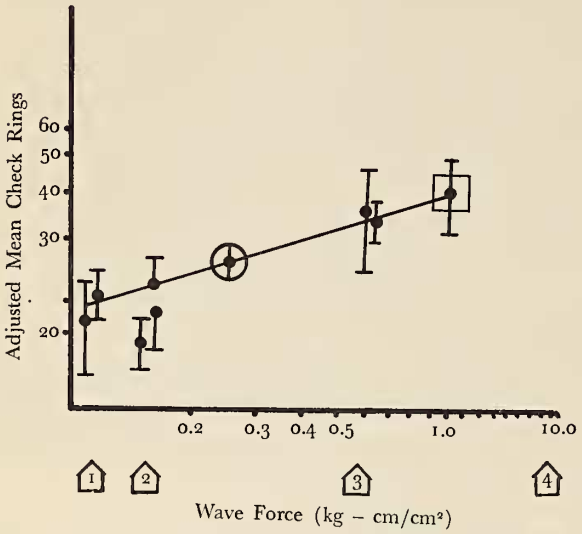

Figure 8

Log log plot of wave force against the mean number of check rings on *Mytilus californianus* shells (adjusted to a shell length of 5 cm) The ○ represents the mean ring frequency for a sample of mussels taken from the outer pilings of a pier at Cayucos Beach, San Luis Obispo County, California. The □ represents the mean check ring frequency for a sample taken from a mid tide rock platform at Monterey Peninsula, Monterey County, California. Both these points have been projected onto a line connecting the points indicating check ring frequency obtained from mussels growing at known wave impact values. The bar representing variation of check rings is proportional to twice the standard error of the mean (on each side).
1. Stearns Wharf 2. outside end of Ellwood Pier
3. Ellwood Shore 4. Goleta Point
The line has been eye-fitted to the points

would probably be established during the time in which longitudinal growth was prevented. In this connection it should be noted that large mussel clumps, attached to Ellwood Pier pilings, move visibly as waves thrust against them; intermittent movement of this kind might allow streams of water to pass through the clumps at some times, but prevent this flow at others.

At least two causal mechanisms seem to be responsible for high frequency ring formation: increased wave impact etc (such as would be experienced by a mussel on the outside of a clump) is one such process; the other seems to be instigated as the result of confinement of animals and the consequent uncertain growth within the matrix of a clump. Such a mussel, so placed within the clump, may experience little growth at infrequent intervals (with each favorable interval providing the small space between the previous ring and that established when conditions favoring elongation are terminated).

Mussels establish rings in response to both factors, but it is possible to distinguish individuals which have developed inside a clump at a glance from those developing on the exterior. The projecting ridges of the rings in the case of the former group tend to be sharply defined, inverted V's, in cross section, whereas the latter group yield rings that tend to resemble inverted U's, in cross section.

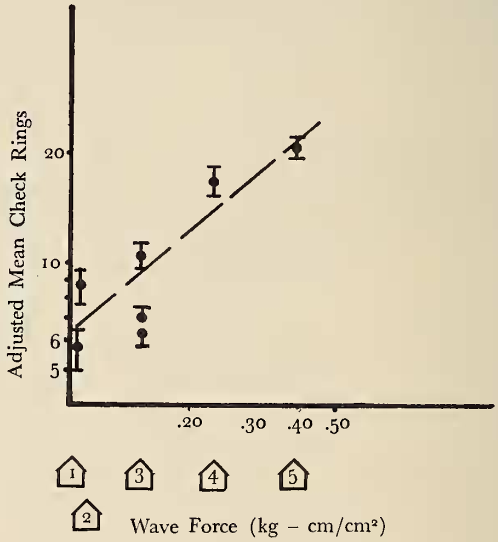

Figure 9

Log log plot of wave force against mean number of check rings on *Mytilus edulis* shells (adjusted to a shell length of 5 cm) The bar representing check ring variation is proportional to twice the standard error (on each side). Station 1 is a submerged electrode cable at Ellwood Pier, 2 is Stearns Wharf, 3 is outside end of Ellwood Pier, 4 the outer end of Cayucos Pier and 5 the inner region (surf zone) of Cayucos Pier, San Louis Obispo County, California. The exposure rating for the outer end of Cayucos Pier (Point A) was obtained from the *Mytilus californianus* exposure plot (Figure 8). The exposure value for the point labeled "inner end Cayucos (Point 5) was obtained by doubling the exposure value for the outer end of this same pier, since the inner regions of Ellwood Pier are about twice as exposed as the outer regions
The straight line was fitted by eye to the points

Table 15

Comparison of the frequency of check rings laid down by *Mytilus californianus* when growing freely high up in the intertidal one (outside top of mussel clumps at Ellwood Pier, two samples), with that frequency shown by mussels growing low in the intertidal on the outside of mussel clumps at Ellwood Pier (Three samples)

The independent variable is growth increment (from February 1966 to 22 June 1966) measured in centimeters and the dependent variable is number of check rings.

Group	N	Regression Equation	Slopes F 4,230	Adjusted Means at X = 1.238	F 4,230
1. Top Pile 26	51	Y=2.9+2.5X	3.73N.S.	6.018	12.71***
2. Top Pile 27	53	Y=1.2+4.2X		6.357	
3. Bottom Pile 26	62	Y=2.3+2.7X		5.739	
4. Bottom Pile 27	42	Y=1.4+2.5X		4.496	
5. Bottom Pile 31	32	Y=1.0+3.5X		5.336	

Individual D. F. Tests on Adjusted Means	F 1,230
1.2./3.4.5	23.92***

It seemed possible that the number of rings per unit shell length could be used as an indication of the amount of harassment mussels had been exposed to during their growth, providing that consideration was lent only to mussels from similar positions within the clumps. The following observations lend further weight to this hypothesis.

If mussels are taken from the outside of the clumps from a fixed intertidal level, a correlation can be established between the wave impact value (measured as reported) to which they have been exposed and the frequency of check rings per 5 cm individual (Figures 8, 9). Such a relationship indicates that the check rings can be used to estimate exposure at a particular place or, more important, to provide an objective method for comparing the exposure between geographical locations. A log log scale was used to plot ring frequency against wave impact value in Figures 8 and 9 because, as shown, the points then fell on a straight line.

As mentioned previously, a lower limit was found to exist for the frequency of check rings a mussel may lay down, and it would seem that an upper limit might also exist. This would be imposed by the width of the rings themselves, i. e., only a fixed number could exist between two points (if one assumes a minimum thickness for a ring). To determine whether the frequency of check rings on mussels can be used to estimate the wave impact experienced by a particular region of shore line, I have plotted in Figure 8 two points representing check ring frequencies obtained from samples of mussels taken from two places where I had not previously obtained wave impact values. The locations were:

1. The outer pilings of a pier belonging to the Standard Oil Company at Cayucos Beach, San Luis Obispo County, California.
2. An intertidal rock platform at Monterey Peninsula, California.

The first point, when projected onto the line connecting the points indicating check ring frequency obtained from mussel populations at known wave impact values, indicates that this pier, located on a section of unprotected coast line, experiences far greater exposure than that experienced by Ellwood Pier.

The second point, I think, probably represents the maximum frequency of growth rings which can occur on a 5 cm mussel growing on the outside of a clump in exposed conditions. By this I mean that, even if mussels were grown in areas which received twice the wave shock experienced by the Monterey mussels, they would be physically incapable of laying down many more rings. In both cases the check ring frequency yields values for the exposure which these populations of mussels experience which is matched by subjective estimates.

A similar relationship between exposure and shell ring frequency exists for *Mytilus edulis* (Figure 9), although this is far less clear than the *M. californianus* example.

Although Barker (1964) has suggested that a positive correlation exists between mean annual temperature and the thickness of growth layers in 3 species of bivalves, *Mercenaria mercenaria, Mactra solidissima* and *Anadara* *ovalis,* his data do not exclude the possibility that turbulence or wave impact have played some part. However, if this correlation reflects the action of temperature as a causative modifying factor in the formation of growth layers then one might expect that mussels growing in colder waters would have more check rings than those growing in warmer waters, all other things being equal.

SUMMARY AND CONCLUSIONS

The wave impact measuring device described provides the intertidal ecologist with a simple method of estimating wave impact at various places. A biological recorder in the form of mussel check ring frequency may also be used where 2 or 3 comparisons are to be made within one particular area. Since several factors are known to affect the frequency of ring production, i. e., height on shore, position within mussel clump, etc, great care must be used when selecting the samples for analysis to ensure that they are taken from comparable positions. I regard a sample of around 50 individuals to be the minimum necessary to establish the mean check ring frequency for any one place. Furthermore, all sizes of mussels directly exposed to wave impact should be equally represented within this sample.

I have indicated that several trends in the morphological characteristics of sea mussels can be linked with changes in wave impact. In a later paper I will show that an understanding of these trends was important in investigating the nature of the competitive interaction between *Mytilus edulis* and *M. californianus* on the coasts of Southern California.

ACKNOWLEDGMENTS

This work forms part of a Ph. D. dissertation presented at the University of California at Santa Barbara. I wish to thank Dr. J. H. Connel, Dr. D. E. Landerberger and Dr. J. Stimson for considerable advice and support. I wish also to thank the Signal Oil and Gas Company for making their premises at Ellwood available for ecological research.

LITERATURE CITED

Ballantine, William
1961. A biologically defined exposure scale for the comparative description of rocky shores. Field Studies 1 (3): 1-19

Barker, Richard M.
1964. Microtextural variation in pelecypod shells. Malacologia 2: 69-86

Bascom, Willard
1964. Waves and beaches, the dynamics of the ocean surface. Anchor Books, Doubleday & Co., Inc. Garden City, N. Y. 267 pp.

Eifion Jones, W. & Andreas Demetropoulos
1965. A quantitative approach to the exposure problem. Br. phycol. Bull. 2 (6): 516-517

Harger, John R. E.
1967. Population studies on *Mytilus* communities. Ph. D. dissertation, Univ. Calif. at Santa Barbara

Li, Jerome C. R.
1964. Statistical inference (I). Edwards Bros., Inc., Ann Arbor, Mich., 658 pp.

Moore, Hilary Brooke
1935. The biology of *Balanus balanoides*. Part IV - Relation to environmental factors. Journ. Marine Biol. Assoc. U. K. 20: 279-307

Southward, A. J. & J. H. Orton
1954. The effects of wave action on the distribution and numbers of the commoner plants and animals living on the Plymouth breakwater. Journ. Marine Biol. Assoc. U. K. 33: 1-19